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The Inheritance of Certain Morphological Characters of the Barley Spike

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THE INHERITANCE OF CERTAIN MORPHOLOGICAL CHARACTERS OF THE BARLEY SPIKE

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INTRODUCTION

Plant breeding, in its simplest form, began thousands of years ago. Since then it has grown into a science of immense practical importance with vast strides made possible by continued research.

The principles upon which plant breeding is based were first set forth by Gregor Mendel in 1865. Prior to this time the fundamentals of genetics as related to plant breeding were not understood and progress was slow. Following Mendel's work, facts have been added to facts and with the knowledge gained, man is better able to meet the requirements of a challenging world. There is a need for fundamental research in the field of plant breeding and through it will come further advances.

Barley, which has 7 chromosome pairs, has been used extensively in these investigations, largely because of its readily classifiable characters. A diploid such as barley offers many advantages for genetic study when compared to similar but polyploid plants.

This paper presents a study of character inheritance and linkage relationships. The main objective of this study is to demonstrate that 2 gene pairs are responsible for hoods and awns in the particular cross studied. Earlier workers have assumed that one factor pair was responsible in most cases. Hoods and awns have been used extensively in linkage studies in group IV but as far as can be determined no earlier workers have reported a 2 factor segregation in regards to hoods and awns with the 2 awn lengths involved.

REVIEW OF LITERATURE

Several workers have attempted to comprehensively review the literature on genetic investigations concerning barley. The most recent attempt was made by Smith (31) who reviewed 1,400 articles, 900 of which were listed in the bibliography. Earlier reviews were made by Daane (7) and Robertson (27) (28).

The review presented here will be confined to the character pairs which are segregating in the cross under study.

Characters investigated

Hoods (K) versus awns (k). According to Litzenberger (19) the barley awn is morphologically a linear extension of vascular tissues of the lemma. Bonnett (4) states that the hood is an accessory flower which on many occasions bears stamens and/or a pistil.

Michels (20) reports that the first hooded barley was found not over 150 years ago near Nepal, India. It was thought to be a mutant from an awned hulless type. Bonnett (4) states that in an F_2 cross between two awned varieties a hooded mutant was found. If the hooded character is dominant it is an example of a dominant mutation. One head in Winter Club barley was half hooded giving in later generations some hooded plants.

Awned varieties usually yield more and shatter less than hooded except when the hooded are hulless. From a practical aspect the study of hoods and awns offers a challenge to plant breeders. Harlan (11) feels that if a hooded barley could be developed which would yield as

well as awned types many more acres of barley would be grown. Rough awned varieties are less desirable because of the bad effects the awns have on animals and products derived from them, such as wool.

In summing up the practical aspects of hoods versus awns, Harlan (11) gives data to show that awns actively function in transpiration and that certain components found in ash may be stored in the awn to be used latter as the plant matures.

The genetic studies involving hoods and awns are numerous, as the character has been used more extensively than any other character in group IV linkage studies. The ease of classification and the almost universal acceptance of the mode of inheritance has made the character very useful in genetic studies.

Smith (31) lists 36 references wherein evidence points to the fact that in crosses between hooded and awned types the F_1 is hooded and in F_2 there are 3 hooded to 1 awned. Investigations at Utah State Agricultural College carried out by Woodward (37) (38), Isom (15), Gill (9), Smith (30), Waddoups (34), and Al-Jibouri (3) support the previously reported F_1 and F_2 phenotypic ratios.

There are in the literature a few studies which indicate that the hood and awn inheritance may not be simple. Lewis (18), summarizing the work accomplished by Von Ubish, shows that 4 gene pairs were responsible for reduced hoods, normal hoods, long awns, short awns, and awnless types. Hoods which developed on short awns rather than on the lemma are referred to as reduced hoods. One factor pair affects awn length only and the other 3 pairs determine the presence of hooded, awned, and awnless forms.

In a cross between hooded and awnless types Myler (21) showed that 3 factor pairs could be responsible for hoods, long awns, short awns, awnletted, and awnless segregates in F_2. When hoods were present all 3 gene pairs had a member in the dominant condition.

It should be born in mind that awnless types do not occur in the cross under consideration and therefore the number of segregating genes could be expected to be less.

Litzenberger (19) states that the factors which determine awn length are located on the same chromosomes as those which determine hoods and awns. He assumes that 2 factors determine awn length while one factor pair determines the presence of hoods or awns.

The work of So, et al., Carne and Limbourn, and Takahashi is reviewed by Smith (31). Their original works were not available but since their material was of interest to this study Smith's (31) review was used. So, et al., found 9:7 ratios in some and 3:1 ratios in other crosses between hooded and awned types. He makes no mention of the type or types of awns which occurred. Carne and Limbourn found hooded, awned, and an intermediate class of hoods on short awns in F_2 progeny of what seemed to be a natural cross between a hooded and awned variety. However, according to Takahashi, normal hoods (K), elevated hoods (K^e), and long awns (k) are governed by an allelic series of genes.

Deficiens (V^t) versus two-rowed (V). The character that determines the species to which a barley belongs affects development of the lateral florets.

Woodward (37) states that genes belonging to 2 multiple allelic series are responsible for the type of fertility which exists in the lateral florets of a barley spike. The confusion which existed in the

literature dealing with this topic was cleared up when Woodward (37) offered conclusive evidence that the number of rows of florets characterising the several types of cultivated barley are determined by an allelic series of 4 genes. These were designated V^t, V^d, V, and v. He showed that the fertility of lateral florets was determined by another allelic series of 3 genes, designated as i, I, and I^h. These allelic series segregate in a simple Mendelian manner and are listed in the order of decreasing dominance. Several workers who agree with Woodward's conclusions on the development of the lateral florets are Fraser (8), Powers (25), Daane (7), Buckley (6), Hanson and Kramer (10), Joachim (16), and Heatby (22).

Earlier, Brussel (5) showed that a cross involving two-row and six-row segregated in a 9:7 ratio in F_2. Robertson (26) and Tedin (33) also suggested that row number is determined by 2 factors.

Crosses involving the six-row gene (v) (which is not present in this study) offer suggestions as to the type of segregation to expect in this cross since it is a member of the allelic series involved.

Harlan (11) states that the problem is complicated by the fact that environmental conditions affect fertility (even of central florets) and also by the fact that two-row barleys occasionally have seeds in lateral florets

Normal (Br) versus brachytic (br). Kramer, Veyl, and Hansen (17) have shown recently that a seventh linkage group has not been located in barley. Before this report the normal versus brachytic (Br br) factor was used extensively in linkage studies and assigned to group VII.

Swenson (32) gives a complete description of a brachytic plant and also reports on its productiveness as compared to normal plants.

In crosses between normal and brachytic plants the F_2 segregation indicates a single factor difference according to Robertson (29), Isom (15), Gill (9), Waddoups (34), Powers (25), Woodward (38), and Swensen (32).

Alternate (Op) versus opposite (op) spikelets. An intensive review of available literature failed to uncover any work dealing with opposite (op) spikelets. An explanation of the character and its expression will be given later. It was found in one of the freak varieties supplied by Harlan and Martini (12).

Lax (L) versus dense (l) spike. According to Wexelsen (35) early workers used laxness of the spike to classify barley varieties. It was not until studies of Harlan and Hayes (13) in 1920 that the length of internode or density was disregarded in barley classification.

Recently Aberg and Wiebe (1) stated that internode length varies a great deal within a variety. They conclude that variations from year to year, place to place, and from spike to spike limit its usefulness as a stable character in variety classification.

Harlan and Hayes (13) report that internode length in a barley spike is a very stable character. The data showed that from one to three factors may be segregating in different crosses. To explain the genetic results they assumed that minor factors were also important in causing segregation.

In a series of crosses Nybom (24) found that the F_1 plants had longer internodes than either parent. He attributed this to overdominance and assumed that one factor pair was responsible for the segregation.

Wexelsen (35) concluded that as many as 6 factors may be involved. His data revealed that transgressive segregation took place and that

the genes involved were dissimilar in their effects. Hor (14) concluded that 2 gene pairs are responsible for the results he obtained in F_2 segregates.

Isom (15), Wheatley (36), Neatby (23), Woodward (38), and Robertson (29) assumed that density is governed by one gene pair. Neatby (23) indicates that modifying factors were operating in his material.

Long glume hairs (Gh) versus short glume hairs (gh). The amount of literature dealing with the length of glume hairs is limited. Aberg and Wiebe (1) (2) state that the length of glume hairs can be used successfully in barley classification because it is a stable character under varying environmental conditions.

Working with 15 different barley crosses Woodward (38) concluded that segregation for length of glume hair was simple, giving a 3:1 ratio in F_2. Al-Jibouri (3) and Isom (15) obtained similar results.

Gill (9) working with glume hair length, found the F_1 to be intermediate between the 2 parents. He found classification in F_2 difficult, thus making it necessary to carry the material to the F_3 generation. A 1:2:1 ratio was obtained with a good fit.

Waddoups (34) observed 3:1, 1:2:1, and 1:1 F_2 ratios for long versus short glume hairs in different crosses. He concluded that the segregation was complicated and that as many as 3 factor-pairs may be responsible for the character.

Linkages

Independent assortment, as first explained, is an important genetic principle. An exception to independent assortment is found when characters which enter a cross together appear together in the offspring more times than chance would allow. When this occurs we

assume there is linkage or that the genes which determine the characters are found on the same chromosomes.

Smith (31) in his review places the gene pair which determines deficiens (V^t) versus two-row (V) in linkage group I, normal (Br) versus brachytic (br) in linkage group VII, and hoods (K) versus awns (k) in linkage group IV. The several genes which have been associated with internode length on various occasions have been reported to be linked with genes in linkage groups I, III, and V. The other characters in this study have not been reported in linkage summaries. If the observations by Kramer (17) are correct then normal (Br) versus brachytic (br) and the factor, or factors, for internode length located on linkage group III should be linked. No information is available on this possible linkage.

Wexelsen (35) and Neatby (22) (23) report linkages involving fertility of lateral florets and internode length. A cross over value of 40 percent was obtained by Wexelsen (35). The linkage found by Neatby (22) (23) was rather weak but he assumed this was to be expected since his data showed 2 or more factors determined internode length.

MATERIALS AND METHODS

In the summer of 1951, Dr. R. W. Woodward made a barley cross involving a short awned brachytic (br) plant which had opposite (op) spikelets and a normal (Br), hooded (K) plant with alternate (Op) spikelets. Plants representative of these parents are shown in figure 1. The F_1 families resulting from the cross were grown during the summer of 1952. At the time of maturity heads from each plant were threshed separately and stored for F2 plantings the next year.

The F_2 plants were spaced at two to three inch intervals in the field to permit easy classification later in the summer. After observing the F_2's during the summer Dr. Woodward decided that the material was important enough to warrant F_3 classification. Each of the 620 F_2 progenies was harvested separately. All 5 families appeared to be segregating in a similar manner so no attempt was made to keep the families separate in F_3. The 620 F_3 plant rows were space seeded in the spring of 1954. At harvest time the rows were tied separately and placed in storage.

Classification of the F_3 plant rows began in November 1954. It was of 2 types, depending on the character under consideration. The most intensive of the 2 types involved the classification of all the individuals in an F_3 row (or bundle). A less intensive type of analysis involved the determination of the genotype of F_2 by determining the type of segregation in the F_3 bundle without studying or measuring individual plants.

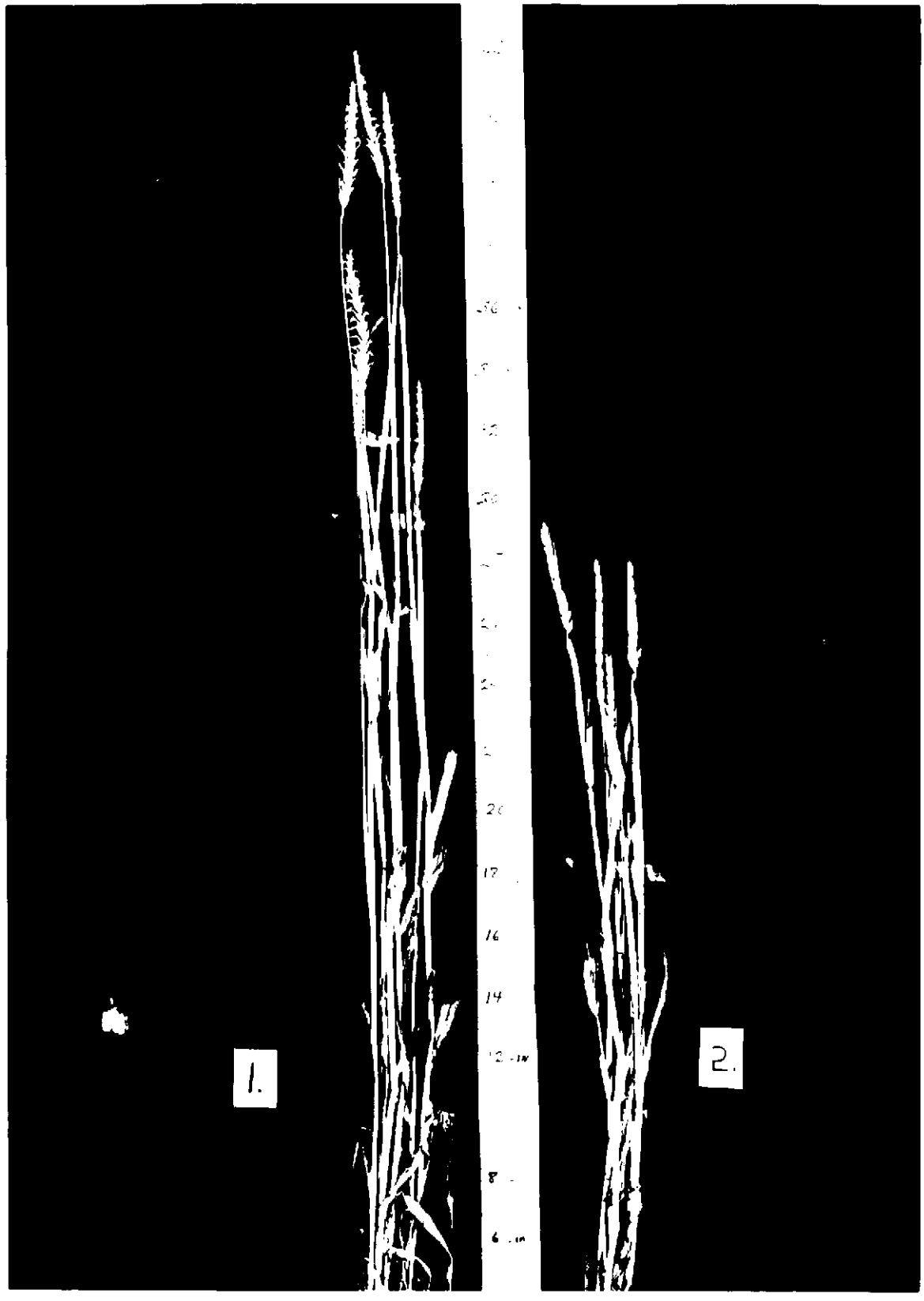

Figure 1. Normal (Br), hooded (K) parent and short (k_2) awned brachytic (br) parent used in this study.

An analysis of data obtained during the winter showed that segregation for glume hair length and alternate (Op) versus opposite (op) spikelets were not fitting Mendelian ratios too well although inheritance of these characters seemed to be simple. They were reclassified in the spring and these data are presented.

Measurements were made on the height of the plants, the length of 10 internodes and the length of awns. The remainder of the data were qualitative in nature.

To facilitate the study several crosses were made in the greenhouse during the winter of 1955 between long and short awned types. The progeny were planted in the field in the spring of 1955. Several plants from the F_3 material were threshed and the seed was also planted. These plantings were observed during the summer as were the F_1's from the above mentioned cross.

The statistical analysis used in this study involve the use of chi-square for goodness of fit and independence with linkages computed by the product method. Unless otherwise specified, chi-square and P values are based on a 3:1 ratio for inheritance and a 9:3:3:1 for linkage values in the F_2 generation.

Characters used in this study, their gene symbol and method of classification

Hoods (K) versus long (k_1) and short (k_2) awns. Measurements of the awn length were taken and the plant was classified as long or short awned. Brachytic (br) plants have much shorter awns than normal (Br) ones, thus making it necessary to determine whether the plant was normal (Br) or brachytic (br) before awn classification could be made. Both long (k_1) and short (k_2) awns were reduced proportionately in

brachytic (br) plants. Figure 2 illustrates the types of hoods and awns found in normal and brachytic plants.

Deficiens (V^t) versus two-row (V). The deficiens (V^t) types have 2 central rows of florets completely fertile but the 4 lateral rows are infertile. Each lateral floret consists of a lemma, rarely a palea and no sexual parts. Two-row (V) types consist of 2 rows of fertile florets and 4 of infertile lateral florets. The lateral florets are of 2 types with the first type having reduced florets which are either all male or sexless and the second type containing the normal components of a floret. They are, however, much reduced in size. The latter type is somewhat larger and more rounded.

The deficiens (V^t) and two-row (V) types are easily identified by the degree of lateral floret development.

Normal (Br) versus brachytic (br). A brachytic (br) plant can be easily recognised by its shortened condition. All components of the plant are shortened correspondingly to varying degrees and the leaf blade is broader, thus aiding in identification. Measurements were taken on all F_3 bundles. Figure 3 contains 3 normal (Br) and 2 brachytic (br) plants.

Alternate (Op) versus opposite (op) spikelets. Plants having opposite (op) spikelets were classified as such when one or more pairs of opposites (op) were found. The occurance of opposite (op) spikelets is not uniform in its expression. On some plants every spike may have several pairs of opposites (op) while on other plants only one spike will have opposites (op). Close inspection of the opposite (op) spikelets on the rachis shows every other rachis internode is shortened and appears to be lacking. The number of opposites (op) on each spike also varies widely. These factors make classification difficult.

Figure 2. Long (k_1), hooded (K), and short (k_2) awned plants. Numbers 1, 3, and 5 are normal (Br); 2, 4, and 6 are brachytic (br).

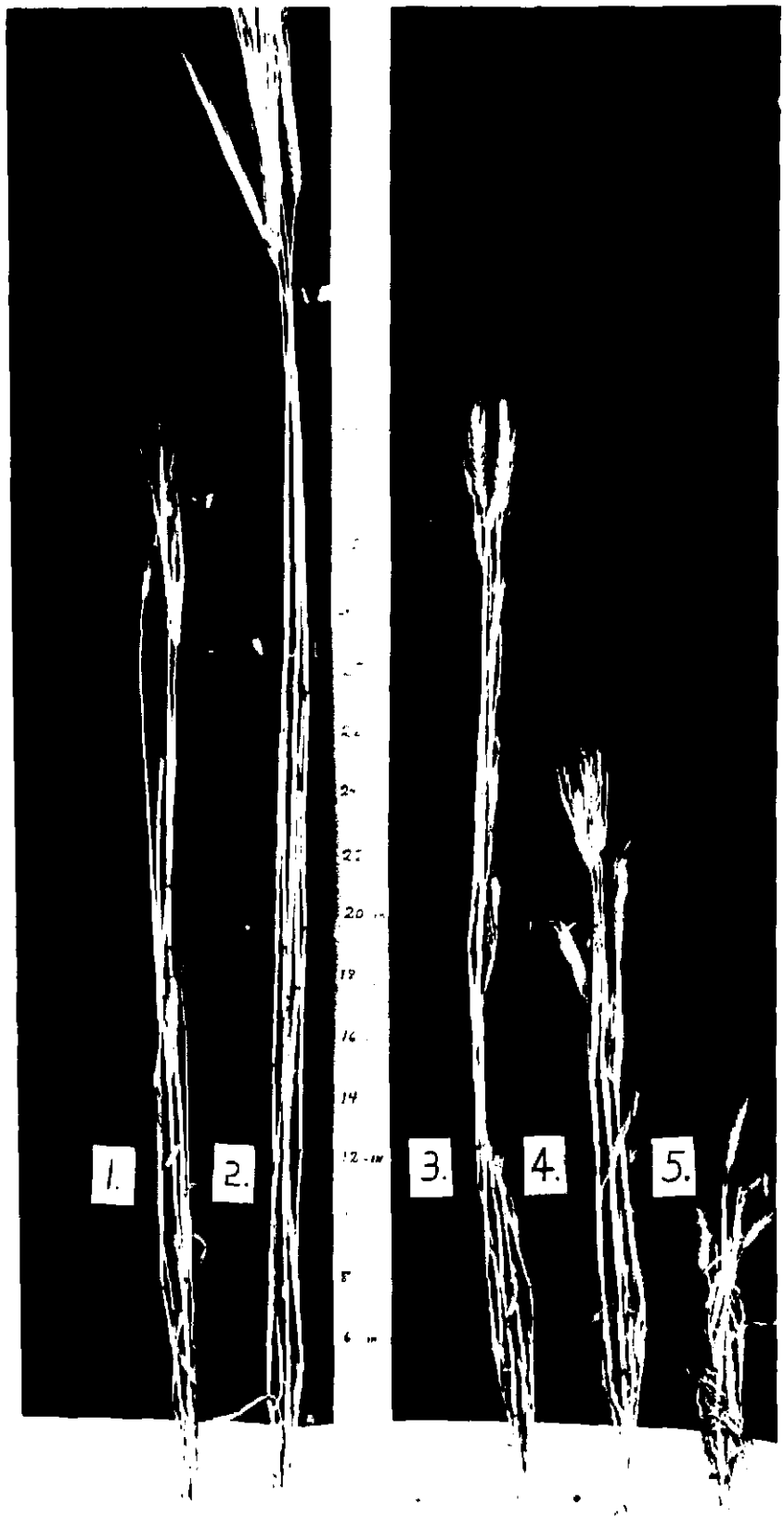

Figure 3. Height segregation found in normal (Br) and brachytic (br) plants. The first 3 plants are normal (Br), the last 2 are brachytic (br).

Figure 4 contains spikes which have several pairs of opposites (op) spikelets.

Lax (L) versus dense (l) spike. Laxness (L) or denseness (l) of a spike is determined by the length of the internode. The length of the internodes was measured from the 10 internodes just above the second node.

Long (Gh) versus short (gh) glume hairs. A small extension similar to the awn found on a barley lemma is found on glumes. Each of the 6 glumes at a node have a glume hair attached. The length of the glume hair in relation to the glume is used in classification. Glume hairs as short or shorter than the glume are classified as short (gh).

Linkage calculations. Linkage studies involving characters which are determined by more than one gene pair in which both pairs are segregating are somewhat complicated. These data are less reliable than studies on linkages in which each character is determined by one gene pair.

Linkages involving hoods and awns are of this more complex type since they contain the (Lk) and (K) genes, each of which is segregating. To check linkages involving these genes it is necessary to compare individuals which are homozygous dominant and homozygous recessive for each of the gene pairs. The other gene pair must be disregarded. It should not alter the results, however, since the genes not being tested are in the same proportion in each homozygous group being tested. This method can be illustrated as follows: The genotypes (KK lk lk) (Kk lk lk) and (kk lk lk) represent the homozygous (lk lk) genes while the (KK Lk Lk) (Kk Lk Lk) and (kk Lk Lk) represents the homozygous (Lk Lk) genes. If assortment is independent then ratios with the

Figure 4. Selected spikes which showed more opposites than ordinarily occurred in this study.

character being tested for linkage will be similar in (Lk Lk) and (lk lk) groups.

Linkages involving glume hair length and opposite (op) spikelets were worked on the basis of 3:1 ratios in the F_2 generation. Since these characters did not segregate in a 3:1 F_2 ratio the value of linkages taken from them will not be considered completely accurate.

EXPERIMENTAL RESULTS

The results presented here are arranged in the same order as in the review of literature. Linkage results for the characters involved follow the data on inheritance.

Inheritance of individual characters

Hoods (K) versus long (k_1) and short (k_2) awns. Analysis of the F_3 population revealed that segregation for hoods (K), long (k_1) and short (k_2) awns in the F_2 is determined by 2 gene pairs. The data presented in table 1 show a near perfect fit to the calculated 9 hoods (K), 3 long (k_1) and 4 short (k_2) awned types.

Table 1. Segregation of hoods, long and short awns. Chi-square and P values based on 9:3:4 ratio in F_2 generation.

Phenotype	Phenotypic Ratio	Expected	Observed	$\frac{(\text{Deviation})^2}{\text{Expected}}$
Hoods	9	348.75	348.00	.002
Long awns	3	116.25	115.00	.010
Short awns	4	155.00	157.00	.030
				$\chi^2 = .042$
				$P = .95 - .98$

Segregation found in 620 F_3 head rows and the 9 genotypes involved in the segregation are given in table 2. Of the 9 genotypes 4 are responsible for hoods (K), 2 for long awns (k_1), and 3 for short (k_2) awned types in F_2. P values found in table 2 indicate that postulated genotypes could easily explain the segregation which occurred.

Table 2. F_2 genotypes and segregation found in 620 F_3 progeny rows

F_2 Genotype	Genotypic Frequency	Segregation in F_3 progeny	Expected	Observed	$\frac{(\text{Deviation})^2}{\text{Expected}}$
KK Lk Lk	1	All K	38.75	38	.02
KK Lk lk	2	K:k_2 (3:1)	77.50	67	1.42
Kk Lk Lk	2	K:k_1 (3:1)	77.50	85	.73
Kk Lk lk	4	K:k_2:k_1 (9:4:3)	155.00	158	.06
kk Lk Lk	1	All k_1	38.75	45	1.00
kk Lk lk	2	k_1:k_2 (3:1)	77.50	70	.73
KK lk lk	1	All k_2	38.75)		
Kk lk lk	2	All k_2	77.50)	155	.03
kk lk lk	1	All k_2	38.75)		

K = Hoods
k_1 = Long awns
k_2 = Short awns

Total X^2 = 3.98
P = .50 - .70

Table 2 reveals that 5 of the F_2 genotypes should breed true in F_3 while 4 of the genotypes should segregate each in a different manner. A total of 14,693 F_3 plants were classified in the 4 segregating groups to determine if segregation fit expected ratios. The results of these counts are presented in table 3. P values are high in 3 segregating groups. Segregation involving long (k_1) and short (k_2) awns have a P value less than .01. A failure to classify awn types correctly in brachytic (br) plants offers an explanation for the significant P value. Data presented in tables 5 and 6 show that if an error in classification occurred it would most likely be found in brachytic (br) plants. Table 4 shows the ratios found in segregates involving long (k_1) and short (k_2) awns when only normal (Br) plants are included in the analysis. In the normal (Br) plants a smaller chance of incorrect classification occurs and the P value is high.

Table 3. Individual plant segregation in F_3 rows

Phenotype	Phenotypic Ratio	Expected	Observed	$\frac{(\text{Deviation})^2}{\text{Expected}}$
Hoods	9	3.719	3.719	.00
Long awns	3	1.653	1.672	.22
Short awns	4	1.240	1.221	.29
				X^2 = .51
				P = .70 - .80
Hoods	3	2.392	2.376	.11
Short awns	1	797	814	.36
				X^2 = .47
				P = .40 - .50
Hoods	3	1.927	1.927	.00
Long awns	1	642	643	.00
				X^2 = .00
				P = .99
Long awns	3	1.741	1.685	1.80
Short awns	1	580	636	5.40
				X^2 = 7.20
				P = <.01

Table 4. Individual plant segregation in F_3 rows involving long (k_1) and short (k_2) awns in homozygous normal (Br) rows

Phenotype	Phenotypic Ratio	Expected	Observed	$\frac{(\text{Deviation})^2}{\text{Expected}}$
Long awns	3	613.5	623	.146
Short awns	1	204.5	195	.441
				X^2 = .587
				P = .900

Awn lengths in normal (Br) plants vary from 8 to 13 centimeters in long (k_1) awned and from 1.2 to 4.2 centimeters in short (k_2) awned plants. For long (k_1) and short (k_2) awned brachytic (br) plants the

range is from 2.7 to 4.5 and 2.2 to 2.1 centimeters respectively. Figure 5 shows extremes in the 4 awn classes which occurred in F_3 progeny. In tables 5 and 6 mean awn lengths and their standard errors in normal (Br) and brachytic (br) plants are presented.

Table 5. Mean awn lengths in centimeters and their standard errors in normal (Br) plants

Phenotype	Mean	Standard Error	N
Long awns	10.36	.204	50
Short awns	2.84	.092	50

Table 6. Mean awn lengths in centimeters and their standard errors in brachytic (br) plants

Phenotype	Mean	Standard Error	N
Long awns	3.78	.141	50
Short awns	1.10	.065	50

A review of data in table 2 shows that for hoods (K) to develop, one or more dominant genes from each gene pair must be present. Long (k_1) awns develop when the factors for hoods (KK) are in the recessive condition and when the genes (Lk Lk) for awn length are in the heterozygous or homozygous dominant condition. Short (k_2) awns appear when the factors for awn length (lk lk) are in a recessive condition. Apparently the recessive (lk lk) genes are epistatic to the genes for hoods (KK). If this hypothesis is correct a long (k_1) awned plant with the genotype (kk Lk Lk), when crossed with a short (k_2) awned

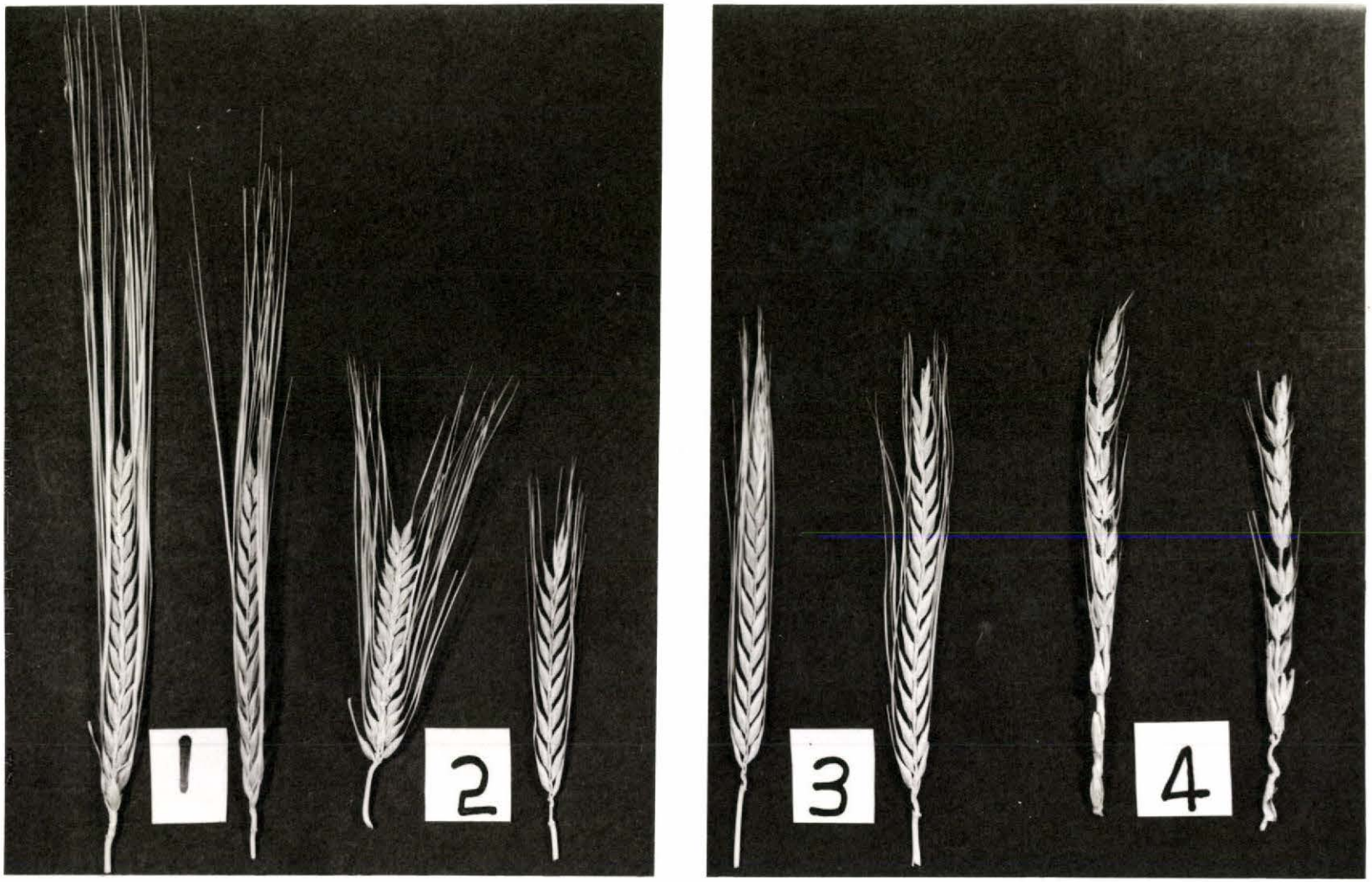

Figure 5. Numbers 1 and 2 show long (k_1) awned extremes and 3 and 4 show short (k_2) awned extremes of normal (Br) and brachytic (br) plants.

plant with a genotype (KK lk lk), will give a hooded plant in F_1. This plant will have a genotype similar to the F_1 of the original cross which was (Kk Lk lk). The results of this cross are shown in figure 6. The two progeny shown represent the extremes in elevated hoods or partially hooded awns.

Deficiens (V^t) versus two-row (V). Data in table 7 show a monofactorial difference between the near dominant deficiens (V^t) and two-row (V) character in the F_2 generation.

Table 7. Data for deficiens (V^t) versus two-row (V) in the F_2 generation

V^t	V	Total	χ^2	P
463	154	617	.003	.98 - .99

Normal (Br) versus brachytic (br). Segregation between normal (Br) and brachytic (br) is determined by one gene pair. Data supporting this point are presented in table 8. Mean heights of the normal (Br) plants range from thirty-four to fifty-two inches. Brachytic (br) plants have means ranging from twelve to thirty-four inches. Plants representative of these extremes appear in figure 3.

Table 8. Normal (Br) versus brachytic (br) plants in the F_2 generation

Br	br	Total	χ^2	P
455	165	620	.86	.30 - .50

Figure 6. Extremes in progeny involving long (k_1) and short (k_2) awned parents.

A random sample of 50 F_3 means was chosen to show mean heights and the standard errors in both the normal (Br) and brachytic (br) groups. These data are presented in table 9.

Table 9. Mean heights in inches of normal (Br) and brachytic (br) plants and their standard errors

Phenotype	Mean	Standard Error	N
Normal	42.6	.39	50
Brachytic	26.3	.54	50

A number of plants grown in F_4 (for observational purposes) suggest that modifying factors may effect plant height. Several tall brachytics (br) with a mean height of about 30 inches seem to be breeding true for this height while other brachytics which measured less than 20 inches in F_3 are also breeding true. Homozygous lines with intermediate heights could likewise be isolated.

Alternate (Op) versus opposite (op) spikelets. Data in table 10 suggest that a simple Mendelian gene may be involved in determining the presence of opposite (op) spikelets. Proof of this simple segregation is lacking and the resulting P value is less than .01.

Table 10. Data for segregation of alternate (Op) versus opposite (op) spikelets

A	a	Total	X^2	P
506	112	618	15.58	$<.01$

Plants grown in F_4 show that the gene, or genes, for opposite (op) spikelets may not have the ability to express the character in some instances. This failure of expression varies from plant to plant and from spike to spike on the same plant. In a few cases the progeny of individuals, supposedly homozygous for the opposite (op) characteristic, show no evidence of opposite (op) spikelets. Inability to express the character when the gene or genes are present can be demonstrated when different spikes of the same plant are examined. One spike, in some instances, may show definite opposites (op) while other spikes on the same plant may only tend towards opposites (op). Many times normal alternates (Op) can be found on other spikes of plants showing opposites (op).

A few examples of spikes taken from F_3 progeny rows which carry several pairs of spikelets which are opposites (op) are shown in figure 4.

Lax (L) versus dense (l) spike. Data in figures 7 and 8 reveal that inheritance of internode length is similar in normal (Br) and brachytic (br) plants. The graphs suggest that several genes affect the length of internodes. Segregation in F_3 head rows support this view, since there are very few homozygous rows in regards to internode length. Figure 9 shows extreme segregation in internode length found in F_3 progeny.

Long glume hairs (Gh) versus short glume hairs (gh). Data in table 11 show that glume hair segregation does not fit a 3:1 ratio. In figure 10 there are 3 types of glume hairs: long, short, and intermediate. The presence of glume hairs which are intermediate in length suggest that 2 or more genes may be responsible or that some modifying factor or factors are present.

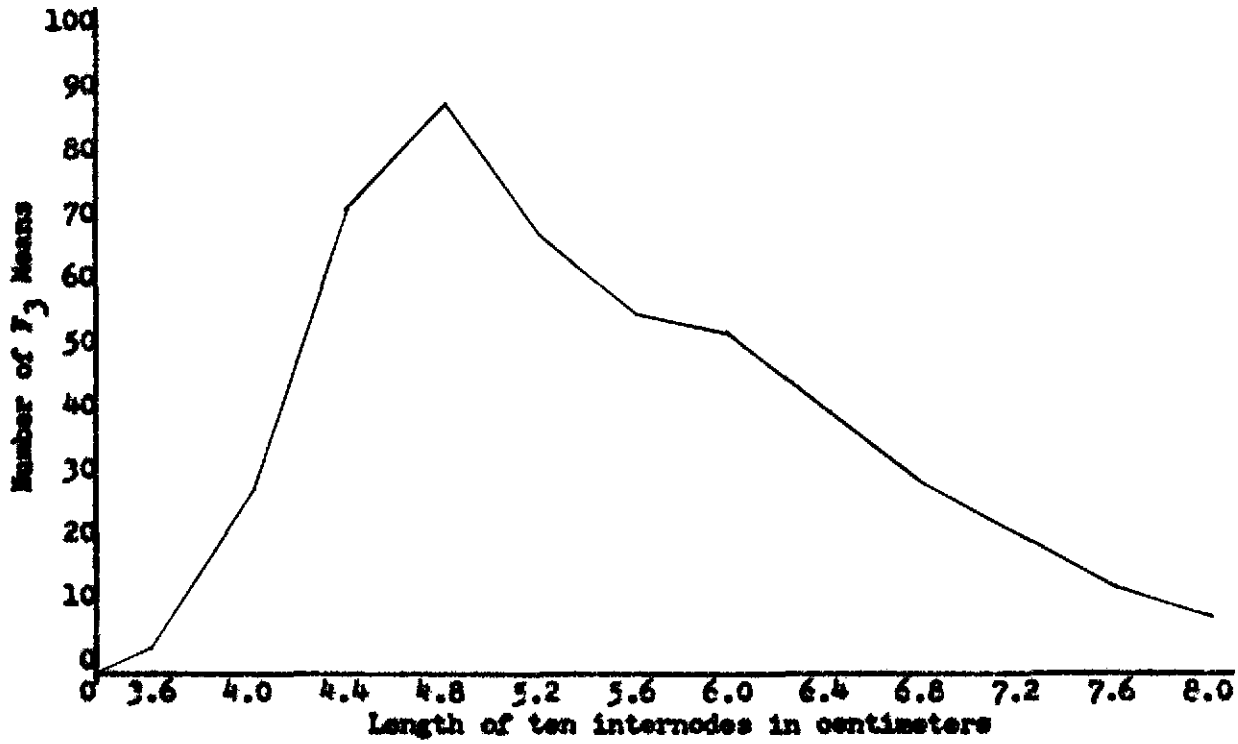

Figure 7. Frequency distribution of internode length in normal (Br) plants. Mean lengths of each of the F_3 progenies are used.

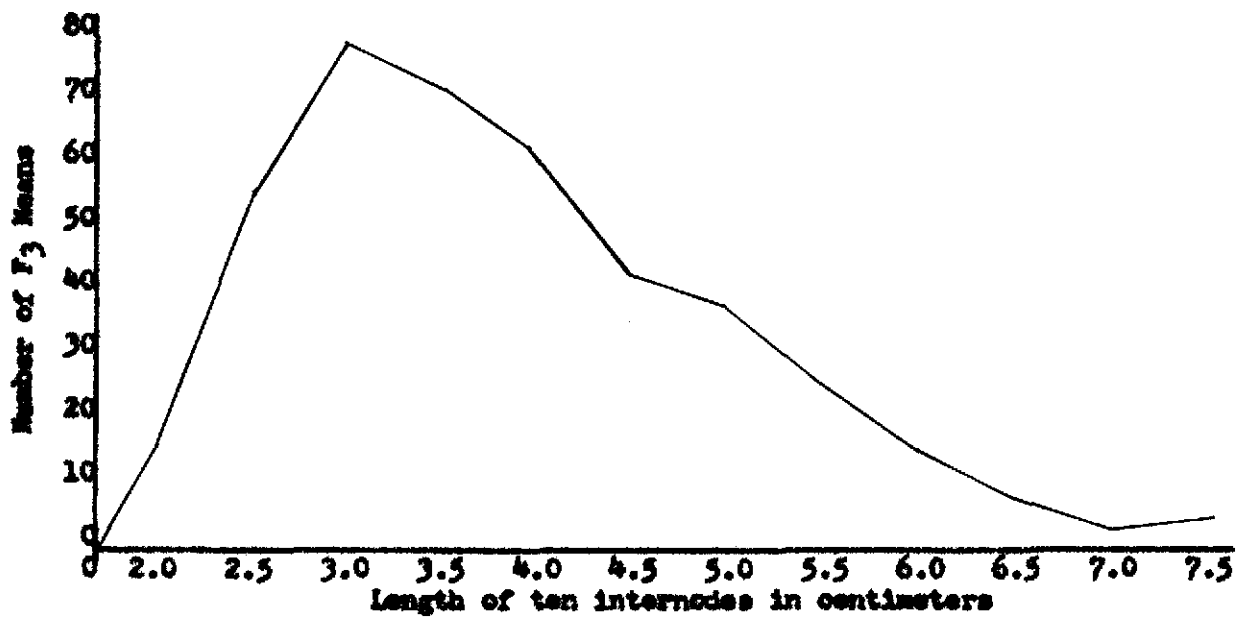

Figure 8. Frequency distribution of internode lengths in brachytic (br) plants. Mean lengths of each of the F_3 progenies are used.

Figure 9. Rachis and spikes showing two extremes in internode length.

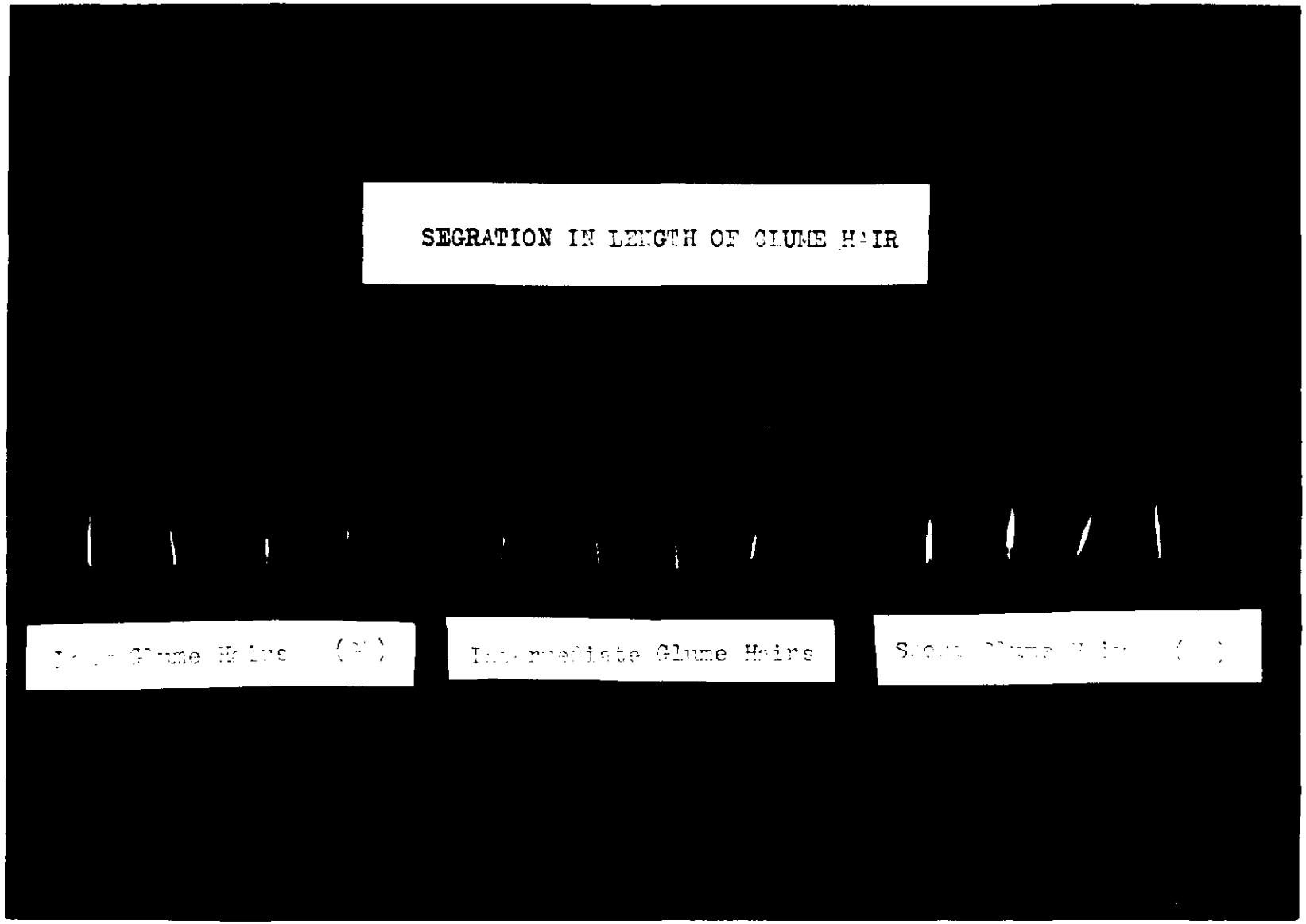

Figure 10. Intermediate glume hair length makes classification difficult.

Results presented in table 11 are suggestive of a simple inheritance and since the intermediate group is in the minority the presence of modifying factors offers a possible explanation.

Table 11. Data for long glume hairs (Gh) versus short glume hairs (gh) in normal (Br) plants

Gh	gh	Total	X^2	P
374	82	456	11.97	$<.01$

Linkage results

Five of the 6 characters reported in this study were checked in all combinations for possible linkages. Density of spike was not used because of the small number of F_2 progeny which were homozygous lax (L) or homozygous dense (l) in breeding behavior.

Characters independently inherited. Deficiens (V^t) was found to be inherited independently of K, Lk, Gh, and Br. Normal (Br) plants were found to occur independently of K, Lk, V^t, and Gh. Characters inherited independently of hoods (K, Lk) are V^t and Op. The occurrence of long (Gh) or short (gh) glume hairs did not effect the ratio of opposite (op) or alternate (Op) spikelets.

Normal (Br) versus brachytic (br) in relation to alternate (Op) versus opposite (op) spikelets. Table 12 presents the factor for normal (Br) plants and the factor or factors for alternate (Op) spikelets. The dominant characters entered the cross from the same parent and tended to remain together in the progeny.

Table 12. Normal (Br) versus brachytic (br) in relation to alternate (Op) versus opposite (op) spikelets

Br-Op	Br-op	br-Op	br-op	Recombination Percent	Standard Error
395	59	111	53	34.5	2.4

Deficiens (V^t) versus two-row (V) in relation to alternate (Op) versus opposite (op) spikelets. The above combinations, when tested in a 2 x 2 chi-square table, showed a small deviation from acceptable P values. Linkage data in the coupling phase show 30 percent recombination using the product method. Data are given in table 13.

Table 13. Deficiens (V^t) versus two-row (V) in relation to alternate (Op) versus opposite (op) spikelets

V^t-Op	V^t-op	V-Op	V-op	Recombination Percent	Standard Error
395	68	112	42	39.0	2.6

The Lk and K genes in relation to long (Gh) versus short (gh) glume hairs. The linkages involving K and Lk genes are computed separately. A 3:1:3:1 ratio is expected when either gene is associated with a character which segregates in a 3:1 ratio. The K and Lk linkages are computed by comparing KK with kk or Lk Lk with lk lk. These genes are not segregating but are in the homozygous condition giving a 1:1 ratio. This cross is in the repulsion phase in regards to the (Gh) character.

The factor for glume hair length seems to be linked with both the Lk and K genes. Tables 14 and 15 contain data which show the extent of the recombination.

Table 14. Long (Gh) versus short (gh) glume hairs in relation to the K gene

K-Gh	K-gh	k-Gh	k-gh	Recombination Percent	Standard Error
61	30	75	8	29.5	6.8

Table 15. Long (Gh) versus short (gh) glume hairs in relation to the Lk gene.

Lk-Gh	Lk-gh	lk-Gh	lk-gh	Recombination Percent	Standard Error
78	30	100	13	35.0	5.8

DISCUSSION AND CONCLUSION

The purpose of this study was to determine the inheritance of hoods (K) and awns (k) in the cross being studied. Abundant data show that inheritance of hoods (K) and awns (k) is determined by two gene pairs. The location of these pairs (KK) and Lk Lk constitutes an interesting study. It is assumed that one gene pair has been segregating while the other pair has been in a homozygous condition in similar studies. Other workers have placed the segregating gene in linkage group IV.

The occurrence of two awn lengths in the F_2 progeny which seems to be determined by the same pair of genes which determine the hooded (K) or awned (k) condition, plus the fact that two genes are involved, makes this study an exception to previously reported data.

The appearance of elevated or awned hoods, rather than normal hoods (K) in an F_1 cross between short (k_2) and long (k_1) awned types, might be assumed to be the result of the heterozygous condition found in the F_1. Whether it is the affect of both K and Lk genes is not known. The type of segregation which occurs in the progeny of this F_1 will be very interesting to follow. By studying these segregates and those obtained from a duplicate of the original cross, it should be possible to determine what causes elevated hoods (K) as compared to sessile. Crosses involving awnless and awnleted types may reveal much needed information regarding the inheritance of several types of appendages found on a barley lemma.

Segregates within brachytic (br) types seem to have different breeding behavior. Some of them breed true for short and some for tall brachytics (br). A cross between these segregates would possibly be informative.

Length of glume hairs is a rather stable character in homozygous varieties but variations in length exist on almost any given spike. This characteristic makes classification difficult. A study aimed at determining the type of segregation on individual spikes may be a helpful preliminary to future investigations. The parents used in this study had glume hairs of unequal length. However, the degree of difference was difficult to determine since the one parent was a brachytic (br) with shortened glume hairs compared to glume hairs on normal (Br) plants. In future studies it would be best to work glume hair length in crosses involving only tall parents with diverse glume hair lengths.

If a character is to be used successfully in inheritance and linkage studies its expression must be similar under varying conditions. This study reveals that the expression of opposite (op) spikelets occur more frequently on brachytics (br) than in normal (Br) plants. This may be due to linkage, but it was noticed that in bundles, presumably homozygous for opposites (op), the normal (Br) plants contained few opposites (op) while brachytics (br) showed few alternates (Op).

The linkage data involving V^t versus Op and Lk versus Gh are very weak and as a result linkages will not be suggested for these characters. The value of linkage data involving characters which are determined by more than one gene pair or on those where the number of genes involved is not known is considerably lessened.

SUMMARY

Six characters were studied in an attempt to determine inheritance and linkage relationship with the major emphasis on inheritance of hoods (K) and awns (k). The F_3 generation used in this study was the result of a cross made in 1951.

An analysis of 620 rows which comprised the F_3 generation revealed that 2 gene pairs were responsible for hoods and awns in this cross. An F_2 ratio of 9 hoods (K), 3 long (k_1) and 4 short (k_2) awned plants occurred. A good fit was obtained to the 9:3:4 ratio which was the result of crossing a hooded (K) by a short (k_2) awned plant. To verify these results a short (k_2) awned plant with the genotype (KK lk lk) was crossed to a long (k_1) awned plant with the genotype (kk Lk Lk). These plants were selected from certain segregating groups which provided the desired genotype. The F_1 from this cross was hooded (K) indicating 2 gene pairs were necessary for the production of a hooded (K) plant.

Deficiens (V^t) versus two-row (V) and normal (Br) versus brachytic (br) were found to segregate in a simple Mendelian manner as previous workers had concluded.

A near normal curve indicated that several factor pairs were effective in determining laxness (L) or denseness (l) of a barley spike.

The inheritance of alternate (Op) versus opposite (op) spikelets and long (Gh) versus short (gh) glume hairs does not fit a monofactorial ratio too well.

Independent inheritance was found between the following factor pairs: Gh, V^{t} and Br; Gh and Op; K and Lk with Op.

Linkages were suggested in the following combinations: (Br, br) in relation to (Op, op) segregating 3:1 and 4.5:1 respectively with a crossover value of 34.5 ± 2.4; (K,k) in relation to (Gh, gh) segregating 1:1 and 4.5:1 respectively with a crossover value of 29.5 ± 6.8.

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